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Forest herbs show species-specific responses to variation in light regime on sites with contrasting soil acidity: An experiment mimicking forest conversion scenarios

Gorik Verstraeten[a,*], Lander Baeten[a], Pieter De Frenne[a], Arno Thomaes[b], Andreas Demey[a], Bart Muys[c], Kris Verheyen[a]

[a]*Forest and Nature Lab, Ghent University, Geraardsbergsesteenweg 267, B-9090 Melle-Gontrode, Belgium*
[b]*Research Institute for Nature and Forest (INBO), Gaverstraat 4, B-9500 Geraardsbergen, Belgium*
[c]*Division Forest, Nature and Landscape, Katholieke Universiteit Leuven, Celestijnenlaan 200E, Box 2411, BE-3001 Leuven, Belgium*

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Abstract

Forest conversion from native deciduous forests to coniferous stands has been performed in many European regions and resulted in dramatic shifts in understorey plant community composition. However, the drivers for changes in specific understorey plant species remained unclear.

Here, we experimentally determine the species-specific effects of light availability and chemical soil characteristics, on the vegetative and regenerative performance of five herbaceous forest understorey plants. Topsoil samples from both spruce and deciduous stands at four locations, with two levels of soil acidity, were collected and used in a common garden experiment. Additionally, three different light levels were applied, i.e., 'light deciduous', 'dark deciduous' (extra light reduction during summer) and 'evergreen' (light reduction during winter). In a second experiment we evaluated the germination of two of these species against the acidity and tree species at the site of origin of the soil samples.

The light regime affected both the vegetative and regenerative performance of the understorey species: compared to light deciduous, *Anemone nemorosa* had a significantly lower performance under the evergreen light regime, *Convallaria majalis* under dark deciduous and *Luzula luzuloides* and *Galium odoratum* under both light regimes. The vegetative performance was lower in soil from acid sites for the acid-sensitive species *G. odoratum* and *Primula elatior*. Differences between the soils sampled under deciduous or spruce stands had no effect on the vegetative, or the regenerative performance of these species. By contrast, the germination of *L. luzuloides* and *P. elatior* was higher in soils sampled in deciduous stands and in neutral sites.

Species-specific responses in vegetative and regenerative performance of adult plants to a changed light regime and soil acidification could be a reason for the changed vegetation composition in converted stands. Also lower germination and establishment of forest understorey species in spruce stands could influence the species distribution after conversion.

Zusammenfassung

Die Umwandlung von natürlichem Laubwald in Nadelbestände wurde in vielen Gebieten Europas durchgeführt und resultierte in dramatischen Änderungen in der Zusammensetzung der Pflanzengesellschaft des Unterwuchses. Indessen sind die

*Corresponding author. Tel.: +32 9264 9035; fax: +32 9264 9092.
E-mail addresses: gorik.verstraeten@ugent.be, kris.verheyen@ugent.be (G. Verstraeten).

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treibenden Faktoren für die Änderungen bei einzelnen Krautschichtarten unklar. Hier bestimmen wir experimentell die artspezifischen Effekte von Lichtverfügbarkeit und Bodenchemie auf die vegetative und regenerative Leistung von fünf Arten der Krautschicht. Proben des Oberbodens wurden in Fichtenforsten und Laubwäldern mit jeweils zwei Aziditätsstufen gesammelt und in einem common-garden-Experiment verwendet. Zusätzlich wurden drei Stufen der Lichtintensität eingesetzt: „heller Laubwald", „dunkler Laubwald" (mit zusätzlicher Beschattung im Sommer) und „Immergrün" (mit Lichtreduktion im Winter). In einem zweiten Experiment maßen wir die Keimfähigkeit von zwei der Arten in Abhängigkeit von Azidität und Baumart am Herkunftsort der Bodenproben. Das Lichtregime beeinflusste sowohl die vegetative als auch die regenerative Leistung der Krautschichtarten: verglichen mit „heller Laubwald" hatte *Anemone nemorosa* eine signifikant geringere Leistung unter dem „Immergrün"-Regime, *Convallaria majalis* unter dem „dunkler Laubwald"-Regime und *Luzula luzuloides* und *Galium odoratum* unter beiden Lichtregimen. Bei den säureempfindlichen Arten *G. odoratum* und *Primula elatior* war die vegetative Leistung in Böden von sauren Standorten geringer. Unterschiede zwischen den Böden, die von Laubwald- bzw. Fichtenstandorten gesammelt worden waren, hatten keinen Einfluss, weder auf die vegetative noch auf die regenerative Leistung dieser Arten. Dagegen war die Keimfähigkeit von *L. luzuloides* und *P. elatior* höher in Böden von Standorten mit Laubwald und neutralem pH. Artspezifische Reaktionen der vegetativen und regenerativen Leistung von adulten Pflanzen auf ein geändertes Lichtregime und Bodenversauerung könnten ein Grund für die geänderte Artenzusammensetzung in umgewandelten Beständen sein. Auch könnte verminderter Keimungserfolg und die Etablierung von Krautschichtarten in Fichtenforsten die Artenverteilung nach der Umwandlung beeinflussen.

Keywords: Species-specific response; Plant performance; Tree species effects; Acidification; Pot experiment

Introduction

The composition of the regional pool of forest plant species is principally controlled by climatological, geographical and geological characteristics (Augusto, Dupouey, & Ranger 2003). At the local scale, the composition of the forest tree canopy, among other factors, plays an extremely important role in determining the understorey species diversity and community composition (e.g. Barbier, Gosselin, & Balandier 2008; van Oijen, Feijen, Hommel, den Ouden, & de Waal 2005; Wulf and Naaf 2009). The ecological characteristics of the tree species and their abundance affect local environmental characteristics important for understorey species, including the amount of light transmittance (Barbier et al. 2008) and leaf litter quality and quantity, influencing several biotic and abiotic soil properties (De Schrijver et al. 2012; Kooijman 2010; Reich et al. 2005). Therefore, changes in the composition of canopy tree species can significantly impact the local understorey species diversity and composition of forests.

During the 19th and 20th century, large areas of native deciduous forests in Western and Central Europe were converted to coniferous plantations, mainly motivated by economic interest (Spiecker et al. 2004). The conversion from native deciduous, broadleaved temperate forests to Norway spruce (*Picea abies*, further referred to as "spruce") plantations is for instance widespread and changed chemical soil characteristics, the forest floor environment and the understorey composition in many European regions (e.g. Ewald 2000; Máliš et al. 2012; Verstraeten et al. 2013). Coniferous tree species contribute significantly to the soil acidification, often more than many deciduous tree species (Augusto, Bonnaud, & Ranger 1998; Augusto, Ranger, Binkley, & Rothe 2002), and also change the understorey light regime. Lower light transmittance is particularly evident in winter and early spring due to their evergreen character. Nevertheless, due to often more frequent thinning in coniferous stands, light transmittance in summer can be in fact higher than in the deciduous stands. The changes in soil, litter and light conditions may cause changes in the understorey community towards more acid-tolerant species with higher light requirements in coniferous stands (e.g. Verstraeten et al. 2013).

Several observational studies stressed the effects of changes in tree species composition on the understorey layer (e.g. Ewald 2000; Kooijman 2010; Mölder, Bernhardt-Römermann, & Schmidt 2008; Van Calster et al. 2007; Wulf & Naaf 2009), yet they mainly reported community-level patterns of change. The influence of tree species conversion on species-specific adult plant performance and germination, on the other hand, are more difficult to study in the field and therefore less explored. Pot experiments allow testing individual species responses to particular environmental factors such as soil acidity (Falkengren-Grerup & Tyler 1993; Tyler 1996), tree species effects (Thomaes et al. 2011) and light availability (Baeten et al. 2010). However, the combination of light regime and acidification and the effect of an evergreen versus deciduous light regime have not been studied yet.

Widespread conversions of native deciduous forests to coniferous plantations over the past decades have led to significant changes in the forest understorey communities of those forests. In this experiment we tested how the altered light regime and soil conditions after conversion might have influenced plant performance. We examined the response of five characteristic herbaceous understorey plant species to variations in light regime (evergreen vs. light and dark deciduous) and tree species induced changes of soil